

they do not absolutely prove, his case—namely, that the surface and bottom *Globigerinæ* are perfectly distinct forms, and that the latter are never to be found off the bottom.

It is impossible for us here to follow the author through the long series of statements put forward by him in support of his view; and we must conclude this brief notice by simply stating that his little pamphlet furnishes a most useful *résumé* of the present state of knowledge on this interesting subject, even apart from the argument which constitutes the foundation of the whole. The book is illustrated with a plate copied from the author's 'North-Atlantic Sea-bed.'

## PROCEEDINGS OF LEARNED SOCIETIES.

### ROYAL SOCIETY.

December 16, 1875.—Dr. J. Dalton Hooker, C.B., President, in the Chair.

“Preliminary Observations on the Locomotor System of *Medusæ*.”  
By G. J. ROMANES, M.A., F.L.S.

#### I. *Movements of the Medusæ.*

The movements of some of the *Medusæ* (e.g. *Sarsia*) appear to be as *voluntary* as are those of insects. Some of the discophorous species of naked-eyed *Medusæ*\*, when threatened with injury, manifest peculiar movements, which are quite distinct from the ordinary locomotor contractions. These movements consist in a very strong and protracted systole, followed by a slow and gradual diastole. This spasm-like series of movements is never performed by any *Medusa* except when the animal is being injured or threatened with injury.

#### II. *Fundamental Observations.*

§ 1. In the case of all the naked-eyed *Medusæ* which I have this year been able to procure (*viz.* thirteen species belonging to six of the most divergent genera) I find it to be true that excision of the extreme periphery of a nectocalyx is followed by immediate, total, and permanent paralysis of the entire organ. The severed margin, on the other hand, continues its rhythmical contractions as vigorously as when it was still *in situ*, and this for many hours after the operation. Among hundreds of observations I have only met with one exception to the otherwise uniform result of this operation. The exception occurred in an individual belonging to the species *Staurophora luciniata*.

\* I adhere to Forbes's classification only because I have not happened to meet with any individuals of the family *Lucernariadæ*.

§ 2. In the case of the covered-eyed Medusæ I have not found the result of the operation just mentioned to be so uniform as it is in that of the naked-eyed Medusæ. Nevertheless this result, although varying greatly in different species and in different individuals of the same species, is, upon the whole, analogous to that which is so remarkable in the case of the naked-eyed Medusæ; that is to say, in the majority of instances excision of the margin of a gonocalyx is followed by a paralysis as immediate and total as is the paralysis similarly caused in a nectocalyx; but the two cases differ in that (a) this is far from being *invariably* the case, and (b) the paralysis of a gonocalyx, even when total for a time, is seldom *permanent*. After periods varying from a few seconds to half an hour or more occasional contractions begin to take place, or the contractions may be resumed with but little change in their character and frequency.

These remarks apply to gonocalyces in general; but they do not apply in equal degrees to all the genera of covered-eyed Medusæ: *i. e.* different genera of covered-eyed Medusæ manifest, in their constituent individuals, different average degrees of paralysis when subjected to the operation we are considering. Of all the species I have come across, *Aurelia aurita* most resembles the naked-eyed Medusæ in the degree to which the locomotor centres are aggregated in the margin of the swimming-organ; for in the case of this species it frequently happens that the paralysis caused by excision of the margin is permanent.

§ 3. In the genus *Sarsia* I find that excision of the eye-specks alone causes a greater degree of paralysis than does excision of the intermediate portions of the margin alone; for while the former operation is usually sufficient to cause temporary and sometimes permanent paralysis, the latter operation never causes either. That all parts of the marginal tissue between the eye-specks, however, are capable of originating impulses to contraction, is proved by the fact that the smallest atom of this tissue, when left *in situ* after all the rest of the margin has been removed, is frequently sufficient to animate the entire nectocalyx.

§ 4. In the covered-eyed Medusæ I find that the concentration of the marginal supply of locomotor centres into the marginal bodies is even more decided than it is in the case of *Sarsia*. Indeed I have no evidence to show that any part of the margin of a gonocalyx, other than the eight lithocysts, has any function of spontaneity to perform; so that all the remarks made in § 2, while stating the effects of removing the entire margin of gonocalyces, are equally applicable to the effects of removing the lithocysts alone. I may add that in the case of *Aurelia aurita*, which from its flattened shape admits of the fairest experiments being made in this connexion, all the spontaneity of the margin, and so in many cases of the entire animal, is without question seated exclusively in the lithocysts\*.

\* In no case, either among the naked- or the covered-eyed Medusæ, is the polypite affected by removal of the periphery of the swimming-organs.

III. *Stimulation.*

§ 1. All the tissues of all the Medusæ are keenly sensitive to all kinds of stimulation. When a swimming-organ is paralyzed by the operation above described, it invariably responds to a single stimulation by once performing that movement which it would have performed in response to that stimulation had it still been in an unmutilated state.

§ 2. (a) To electrical stimulation, both of the direct and of the induced current, the severed margins and the swimming-organs from which they have just been removed are responsive. There is an important difference, however, between the two cases, in that while the severed margins continue responsive to induction-shocks after they have ceased to be affected by make and break of the direct current, the reverse is true of the mutilated swimming-organs—these continuing responsive to make and break of the direct current after they have ceased to be affected by strong induction-shocks, or even by Faradaic electricity with the secondary coil pushed to zero (one cell).

(b) By means of a DuBois-Reymond induction-apparatus and of needle-point terminals (the needle being passed through a small piece of cork as a support, and the cork being fixed to stage-forceps on the mechanical stage of a Ross microscope), I was able to investigate the distribution of excitable tracts in *Sarsia*. I found that there is an uninterrupted increase of excitability from the apex to the base of the nectocalyx, that the positions occupied by the radial tubes are tracts of comparatively high excitability, that the eye-specks are the most excitable portions of the margin, and that of the eye-specks the vesicular half is more excitable than is the pigment half.

(c) When the marginal rim of any Medusa is removed in a continuous piece, with the exception of one small part, the result, of course, is a long strip of marginal tissue, which is free at all points save at the end which is left attached *in situ*. Upon now irritating the distal end of this marginal strip, a wave of contraction may invariably be seen to start from the point at which the irritation is applied, and with some rapidity to traverse the entire strip. When this contractile wave arrives at the proximal or attached end of the strip, it delivers its influence into the swimming-organ, which thereupon contracts in exactly the same manner as it does when itself directly irritated. Of course spontaneous contractions are always originating in some portion or other of the severed strip; and these give rise to contractile waves and to contractions of the swimming-organ just in the same way as do the disturbances originated by stimuli. In such of the discophorous species of naked-eyed Medusæ, however, as respond to stimulation by the peculiar spasmodic movements of the nectocalyx already described, the difference between the effects upon the nectocalyx of contractile waves which originate in the severed strip spontaneously, and those which there originate in answer to stimula-

tion, is of a very marked character ; for the spasmodic movements of the nectocalyx are as easily and as certainly excited by irritating any part of the severed strip as they are by irritating the substance of the nectocalyx itself.

From this description it will readily be seen that a Medusa, when thus operated upon, supplies all the conditions required for conducting experiments in electrotonus : the animal in this form is, for all practical purposes, a nerve-muscle preparation. Accordingly I have spent a great deal of labour over this part of my subject, but with no very satisfactory results. In the case of *Staurophora laciniata*, however, I have sometimes obtained decided indications of kathelectrotonus, but never any of anelectrotonus. I cannot yet speak decidedly with respect to Pflüger's law.

(d)  $\alpha$ . The excitable tissues of Medusæ, although somewhat capricious in the comparative sensitiveness they show to make and break of the current, upon the whole conform to the rules which are followed by the excitable tissues of other animals.

$\beta$ . Different species of Medusæ manifest differences in the degree of their sensitiveness to electrical stimulation. In all cases, however, the degree of sensitiveness is wonderfully high.

$\gamma$ . When the constant current is passing in a portion of a strip of a severed margin, the nectocalyx sometimes manifests uneasy motions *during the time the current is passing* ; this, however, is perhaps due to variations in the intensity of the current.

$\delta$ . When the intrapolar portion of the severed margin of *S. laciniata* happens to be *spontaneously* contracting prior to the passage of the constant current, the moment this current is thrown in such spontaneous contractions usually cease, and are seldom resumed until the current is again broken, when they are almost sure to recommence. This inhibitory effect may be produced a great number of times in succession.

$\epsilon$ . *Exhaustion* of the excitable tissues may be easily shown by the ordinary methods. Exhausted tissue is much less sensitive to stimulation than is fresh tissue, and, so far as the eye can judge, the contractions are slower with the period of latent stimulation prolonged.

$\zeta$ . *Tetanus* produced by Faradaic electricity is not of the nature of an apparently single prolonged contraction (except, of course, such of the naked-eyed Medusæ as respond to all kinds of stimuli in this way), but that of a number of contractions rapidly succeeding one another. There is hence no appearance of *summation*.

$\eta$ . When the swimming-bell of *Sarsia* has had its margin removed, and so (as proved by hundreds of experiments) has been entirely deprived of its locomotor centres, nevertheless, in response to electrical stimulation, instead of giving a single contraction to make or break, it may begin a highly peculiar motion of a flurried, shivering character, which lasts without intermission for periods varying from a few seconds to half an hour. I never but once saw a similar motion in a perfect animal ; and this was in the



case of a specimen which was being poisoned with iron-rust. The motion may, I think, be explained by supposing that the various systems of muscles are contracting without coordination; but why they should sometimes do this in response to electrical stimulation, and why, when they do this, they should continue the action so long, these questions I cannot answer. In no other genus of the Medusæ have I ever seen a similar or corresponding action performed; and even in the genus *Sarsia* its occurrence is comparatively rare. It never begins spontaneously, and it appears to be most readily evoked by submitting the paralyzed nectocalyx to a number of shocks, either from the direct or the induced current, in somewhat rapid succession. When it does occur it is always continuous, *i. e.* it never spontaneously recommences after having once ceased. When its period of duration is prolonged, the shivering motions become feebler and feebler, until they eventually fade away into quiescence. The animal is then quite insensible to all further stimulation: the tissues appear to have died from exhaustion. These shivering motions may also be caused in *Sarsia* by slightly acidulating the water in which the mutilated nectocalyx is suspended.

§ 3. In their behaviour towards chemical stimuli, the excitable tissues of all the Medusæ conform in every respect to the rules which are followed by the nervo-muscular tissues of higher animals. Both the severed margins and the mutilated swimming-organs, as well, I may add, as severed polypites and tentacles, respond to applications of various acids, solutions of various metallic salts, alcohol, ether, glycerine, &c. Fresh water is quickly fatal to Medusæ.

§ 4. My observations upon thermal stimulation are, for the present, reserved.

#### IV. Section.

§ 1. The extent to which the swimming-organs of Medusæ may be mutilated without suffering destruction of their physiological continuity is in the highest degree astonishing.

(a) Suppose the annexed diagram to represent *Sarsia* in projection, the lines being cuts. It is evident that a stimulus originating at any point *a* in the margin cannot radiate its influence throughout the nectocalyx, except by traversing the course of the dotted line; yet in a specimen so cut the spontaneous contractions are as synchronous over the entire nectocalyx as they are in uncut specimens. Further,



if the margin be now removed, the paralyzed bell will respond to stimuli applied at any part, just as readily and simultaneously over its whole extent as it would do were there no system of interdigitating cuts present.

(b) If the margin of *Sarsia* be removed in a continuous strip, with the exception of one end left attached *in situ*, and if the section be then continued in the form of a spiral having two or more turns from the base to the apex of the cone, the contractile waves originating in the free portions of the severed margin pass into the spiral upon reaching its point of origin, and then run round and round the spiral from the base to the apex of the cone. If the marginal strip be now removed altogether, the paralyzed bell will respond to stimuli applied to any part of the spiral.

(c) If seven lithocysts be removed from the gonocalyx of *Aurelia aurita*, and if the remaining one be made the point of origin of a spiral section, which is then carried round and round the disk-shaped gonocalyx, the result is a long strip of contractile tissue, the contractile waves always originating in the lithocyst at the end of the strip, and then running along the strip until they deliver themselves into the remainder of the gonocalyx, which thereupon contracts. The length and width of such contractile strips are very important factors in determining whether the waves pass all the way along the strip or become blocked at some point in its length. Nevertheless these are very far from being the only factors, there being immense individual differences in the endurance of the contractile tissue under this form of section. Sometimes the waves will become blocked when the strip is only an inch or less in length; while at other times the waves will pass freely from end to end of a contractile strip which is only an inch wide and a yard long.

§ 2. How are the impulses transmitted from the locomotor centres of Medusæ to the contractile tissues of their swimming-organs? Have we any evidence of more or less definite lines of discharge being present? or must we conclude that the contractile tissues are, throughout their extent, of a functionally homogeneous nature?

(a) The fact that the contractile tissues endure such severe section without losing their physiological continuity, appears to settle this question in favour of the last-mentioned alternative. Nevertheless there is a weighty body of evidence to be adduced on the other side. In the first place, the extreme variations in their tolerance of spiral section which are manifested by different individuals of the species *Aurelia aurita* appear to be irreconcilable with the hypothesis of the tissue concerned being functionally homogeneous. But the following invariable fact is still more difficult to reconcile with this hypothesis, viz. *at whatever point in a contractile strip that is being progressively elongated by section the contractile wave becomes blocked, the blocking is sure to take place completely and exclusively at that point.* In view of these facts, therefore, at the present stage of my inquiries, I provisionally accept the hypothesis of more or less definite lines of discharge being pre-

sent in the swimming-organs of *Medusæ*. I have hitherto failed, however, to detect any such lines histologically.

(b) After the waves have become completely blocked in a contractile strip, it sometimes happens that the blocking is overcome, the waves again passing into the remainder of the gonocalyx as freely as they did before the section reached the point at which the blocking occurred. Sometimes, under these circumstances, the strip will admit of being further elongated for some distance before the waves are again blocked; and occasionally it happens that the second blockage is also thrown down. I have once seen four such successive blockages successively overcome.

It will be seen that these facts militate against the supposition of lines of discharge being present. I think, however, that there is a theory by which these facts admit of being satisfactorily reconciled with that supposition. But this whole subject awaits further and extensive investigation.

(c) Pressure exerted upon any transverse line in a contractile strip causes blocking of the waves at that line. If the pressure be slight, the blocking will be temporary; but if severe or long-continued, the blocking will probably be permanent. Even the slight strains caused by handling contractile strips in the air are often sufficient to show the rate of the waves, and sometimes to block them.

#### V. *Additional Facts tending to show the identity of the Locomotor Centres of Medusæ with Nervous Tissue in general.*

§ 1. Having placed several hundred *Sarsie* in a large bell-jar, I completely shut out the daylight from the room in which the jar was placed. By means of a dark-lantern and a concentrating-lens, I then cast a beam of light through the water in which the *Sarsie* were swimming. From all parts of the bell-jar the *Sarsie* crowded into the path of the beam. The presence of a visual sense in the case of this genus is therefore unquestionable.

Having removed twelve vigorous specimens from the large bell-jar and placed them in a smaller one, I excised the so-called eyespecks from nine of the number. The three unmutated individuals sought the light as before; but the other nine swam hither and thither without paying it any regard. I conclude, therefore, that the visual faculty is lodged exclusively in the marginal bodies.

Lastly, I brought a heated iron, just ceasing to be red, close against the glass side of the large bell-jar; but no one of its numerous occupants approached the heated metal. Therefore the rays by which the *Sarsie* had been affected in the previous experiment were the properly luminous rays, and not the calorific ones.

§ 2. (a) The anæsthesiating influence of chloroform and ether is most decided, both in the case of the naked- and of the covered-eyed *Medusæ*. The first indications of approaching torpor are (a) decrease in the rate of the pulsations and (b) diminution of their vigour. These indications rapidly become more and more marked,

o that shortly after they first set in the period of diastole is very much prolonged and the systoles, when they occur, are of the feeblest character. Eventually the pulsations altogether cease; and shortly after this stage of perfect quiescence has been reached, the Medusa is quite insensible to all stimulation. Recovery in normal sea-water is very rapid, occupying only a few seconds in the case of *Sarsia*; but, like the reverse process of anæsthesiation, it is clearly of a gradual nature.

(b) Morphia is as decided in its action upon Medusæ as is chloroform. The processes of anæsthesiation and of subsequent recovery are very similar to those just described, except that both processes occupy a somewhat longer time.

(c) Strychnia exerts a very marked influence upon Medusæ. Of the species I have met with *Cyanæa capillata* is the most suitable for showing the effects of this poison, from the fact that, in water kept at a constant temperature, the normal pulsations of this animal are as regular as are those of a heart. Shortly after a solution of strychnia has been added to the water in which a specimen of *C. capillata* is contained, unmistakable signs of irregularity in the pulsation of the animal supervene. This irregularity then increases more and more, until at last it grows into well-marked convulsions. The convulsions manifest themselves in the form of extreme deviations from the rhythmical character of the normal contractions, amounting, in fact, to nothing less than tonic spasms. It is further of importance to remark that the convulsions are very plainly of a paroxysmal nature—prolonged periods of uninterrupted convulsions being every now and then relieved by shorter periods of repose, during which the Medusa remains perfectly motionless in a fully expanded form. *C. capillata* will live for many hours when under the influence of strychnia, but eventually death supervenes. The animal dies in full diastole.

(d) Curare was administered by the following method. I placed the Medusa in a flat-shaped beaker filled to the brim with sea-water. This beaker I then placed in a large basin filled with sea-water up to the level of the water in the beaker. Having next divided the Medusa across its whole diameter, with the exception of a small piece of marginal tissue to act as a connecting-link between the two resulting halves, I transferred one of these halves to the water in the basin, leaving the other half still in the beaker. Lastly, I poisoned the water in the beaker with successive doses of urari solution. The species best suited for this experiment is *Staurophora lucinata*.

The effects of curare thus administered are most marked and beautiful. Previous to the administration of the poison both halves of the divided Medusa are, of course, contracting vigorously—the contractile waves now running from the half in the basin to the half in the beaker, and now *vice versâ*. But after the half in the beaker has been effectually poisoned all motion in it completely ceases, the unpoisoned half, however, continuing to contract independently. If the poisoned half be now irritated, by nipping with



the forceps or otherwise, it does not itself move, but the other or unpoisoned half immediately responds to the stimulation. If *S. laciniata* be the species of Medusa employed, this result is particularly well marked, from the fact that the unpoisoned half responds to the stimulation by performing the highly distinctive spasmodic movements already described. I have also satisfied myself that curare asserts its peculiar influence upon individuals of the covered-eyed Medusæ. In all cases overpoisoning paralyzes the excitable as well as the motor system. The strength of the solution I used was 1 in 2500, and in this solution the poisoned half required to soak for half an hour.

(e) If any sized portion of a contractile strip cut from the gonocalyx of *A. aurita* be immersed in a sea-water solution of any of the above-mentioned anæsthesiating substances, the contractile waves in the poisoned portion of the strip are first progressively slowed and finally blocked. Upon now restoring the poisoned portion of the strip to normal sea-water, the contractile waves again begin to pass, and eventually do so as freely as before.

If any of the nutrient tubes which cross such a contractile strip transversely be injected with a solution of any of the narcotic poisons, the contractile waves become blocked at the line occupied by that tube. If a discharging lithocyst be similarly injected, it ceases its discharges. From the effects of chloroform and weak solution of morphia, however, it recovers in the course of a night. Alcohol so injected at first causes an increase in the frequency and potency of the discharges, and afterwards progressive torpor. In time, however, the torpidity wears away, and finally the Medusid returns to its normal state.

### GEOLOGICAL SOCIETY.

February 2nd, 1876.—John Evans, Esq., F.R.S., President,  
in the Chair.

“Evidence of a Carnivorous Reptile (*Cynodracon major*, Ow.) about the size of a Lion, with Remarks thereon.” By Prof. Owen, C.B., F.R.S., F.G.S., &c.

The specimens described by the author consist of the fore part of the jaws and the left humerus of a reptile obtained from blocks of Triassic(?) rock from South Africa, forwarded by the late Mr. A. G. Bain, F.G.S. The upper jaw displays a pair of enormous canine teeth, much resembling those of *Machairodus*, being of a very compressed form, with the hinder trenchant margin minutely toothed. There is no dentated border to the fore part of the crown. No teeth can be detected in the alveolar border of the right ramus of the lower jaw, which extends about an inch behind the upper canine. In the symphysial parts of the lower jaw the bases of eight incisors and of two canines are visible, the latter rising immediately in front of the upper ones, to which they are very inferior in size, and being separated by a diastema from the incisors. In this character,